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Using Ecological Theory to Guide the Implementation of Augmentative Restoration¹

ERIN C. BARD, ROGER L. SHELEY, JEFF S. JACOBSEN, and JOHN J. BORKOWSKI²

Abstract: Successful control of invasive plants can have unexpected effects on native plants and wildland systems. Therefore, it is important for managers of invasive species to be concerned with ecological mechanisms and processes like invasion resistance, environmental heterogeneity, and succession that direct plant community dynamics. Augmentative restoration is a management approach for restoring desired species on wildlands dominated by invasive plants, where functioning ecological processes are maintained by selectively augmenting only those processes that are not operating sufficiently. The study was conducted within the Mission Valley, Montana, in an area where meadow vole disturbance provided site availability for colonization. In a split-plot design with four replications, eight factorial treatment combinations from three factors (shallow tilling, watering, and seeding) were applied to whole plots, and 2,4-D was applied to subplots. Cover and density of seeded species, spotted knapweed, and sulfur cinquefoil were sampled in July 2002 and 2003 to produce pretreatment and posttreatment data. Analysis of covariance was used to analyze cover and density data using pretreatment data as a baseline covariate. Data indicated that in areas with adequate site availability due to meadow vole disturbance, seeding and watering without tilling were required to increase seeded species. Spotted knapweed and sulfur cinquefoil decreased in response to 2,4-D. These data provided evidence that augmentative restoration may improve our ability to establish desired species on invasive plant-dominated wildlands.

Nomenclature: 2,4-D; spotted knapweed, *Centaurea maculosa* Lam.; sulfur cinquefoil, *Potentilla recta* L.

Additional index words: Environmental heterogeneity, invasive weeds, native plant establishment, successional management.

Abbreviations: ANCOVA, analysis of covariance.

INTRODUCTION

Successful control of invasive plants can have unexpected effects on native plants and wildland systems. Therefore, it is important for managers of invasive species to be concerned about ecological mechanisms and processes like invasion resistance, environmental heterogeneity, and succession that direct plant community dynamics. Establishing and maintaining invasion-resistant plant communities involve restoring functionally diverse species that promote continuous resource capture, making fewer resources available for invasive species (Carpinelli

et al. 2004; Fargione et al. 2003; Pokorny 2002). Environmental heterogeneity is considered by many ecologists a valuable ecological mechanism that can help explain and predict species composition and even maintain functionally diverse species in many systems (Huston 1994; Loreau et al. 2003; Pickett and Cadenasso 1995). Successional processes regulate plant community change over time. By manipulating successional processes, plant communities may be directed toward functionally diverse, weed-resistant populations (Sheley and Krueger-Mangold 2003; Sheley et al. 1996; Whisenant 1999).

Augmentative restoration is a management approach for restoring desired plant communities on wildlands dominated by invasive species, which is based on theories of invasion resistance, environmental heterogeneity, and succession. We define augmentative restoration as a strategy that enhances ecological processes occurring at sufficient levels by selectively augmenting those processes that occur at inadequate levels to direct plant com-

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² Research Graduate Assistant, Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717; Rangeland Weed Ecologist, U.S. Department of Agriculture, Agricultural Research Service, Burns, OR 97720; Dean and Director, College of Agriculture, Montana State University, Bozeman, MT 59717; Associate Professor, Mathematical Sciences, Montana State University, Bozeman, MT 59717. Corresponding author's E-mail: ebard@montana.edu.

munities in a desirable direction (Bard et al. 2003). Augmentative restoration is based on a successional framework proposed by Pickett et al. (1987) that includes the three causes of succession (site availability, species availability, and species performance), processes that influence these causes, and factors that modify these processes (Table 1). This framework can provide a basis for studying and designing successional management strategies at different sites.

Manipulation of the three causes of succession involves (1) designing disturbances to create or eliminate site availability for particular plant species, (2) controlling colonization to decrease or enhance availability and establishment of specific species, and (3) controlling species performance to decrease or enhance the growth and reproduction of particular species (Luken 1990). In some cases, it may not be necessary to manipulate all the three causes of succession. For example, natural disturbances may provide adequate bare soil microhabitats for colonization of desired species (Bazzaz 1996; Walker and del Moral 2003). In these cases, designing a disturbance may not be necessary, but controlling colonization and species performance may be required for establishing desired plant communities.

This study was conducted within an area characterized with high levels of meadow vole (Microtis pennsylvanicus Ord.) disturbance, low cover of native species, as well as low soil moisture. Substantial evidence indicates that small-mammal disturbance creates new opportunities for species establishment by removing established plants and litter while tilling the soil (Hobbs and Mooney 1985; Kotanen 1997; Rebollo et al. 2003). Controlling the species available for colonizing these areas may be important so that desired species establish rather than exotics like spotted knapweed and sulfur cinquefoil (Kotanen 1997). Therefore, broadcasting a functionally diverse desirable seed mixture that may reduce resource availability to spotted knapweed and sulfur cinquefoil may be necessary (Carpinelli et al. 2004; Fargione et al. 2003; Pokorny 2002). Increasing soil moisture levels also may be important to favor the performance of desired species while reducing the performance of invasive species. LeCain (2000) found that spotted knapweed establishment and growth was inhibited in areas with high soil moisture such as transitional zones between wetland and upland areas.

Herbicidal control of spotted knapweed and sulfur cinquefoil may enhance the emergence and establishment of seeded species by reducing competition from these invasive plants (Sheley et al. 2001). Herbicides

could influence all the three causes of succession by increasing site availability when particular species are removed, shifting species availability with the removal of certain species, and influencing species performance of different species within the plant community. The herbicide 2,4-D is used for broad-spectrum control of broadleaf weeds and provides about 90% control of spotted knapweed and sulfur cinquefoil for up to 1 yr (Dewey et al. 1997). Its short half-life and soil-binding properties can minimize negative effects on desired species. A fall application of 2,4-D could target fall growth of spotted knapweed and sulfur cinquefoil when desired species are dormant (Jacobs and Sheley 1999).

Our first objective for this study was to determine the response of broadcast seeding to influence species availability and watering to influence species performance in areas with adequate site availability due to meadow vole disturbance on seeded species. We hypothesized that broadcast seeding combined with watering would augment areas with existing vole disturbance to increase seeded species. Our second objective was to determine the effects of a fall application of 2,4-D on spotted knapweed and sulfur cinquefoil as well as seeded species. We hypothesized that a fall application of 2,4-D would reduce spotted knapweed and sulfur cinquefoil without reducing seeded species.

MATERIALS AND METHODS

Study Site. The study was conducted within the Kicking Horse Wildlife Mitigation Area located in the Mission Valley north of Missoula, MT (47°29′N, 114°5′W). This area is characterized by ephemeral wetlands and lies on a rough fescue (*Festuca scabrella* Torr.)—bluebunch wheatgrass [*Agropyron spicatum* (Pursh) Scribn. & Smith] habitat type (Mueggler and Stewart 1980) dominated by spotted knapweed and sulfur cinquefoil. The study site is located in an upland area with substantial meadow vole disturbance. Precipitation averages 400 mm/yr, and the mean annual temperature is 7.6 C. The soil is a well-drained silt loam and silty clay loam (glaciolacustrine deposits) with sodic properties within the top 76 cm. The slope varies from 2 to 15%, and the elevation is 940 m.

Treatments and Experimental Design. In a split-plot design with four replications, eight factorial treatment combinations from three factors (shallow tilling, watering, and seeding) were applied to whole plots (2 m²) and 2,4-D was applied to subplots (1 m²). Shallow tilling, seeding, and 2,4-D were applied in the fall of 2002. In late September 2002, 2 kg ae/ha of 2,4-D was applied

Table 1. Causes of succession, contributing processes, and modifying factors.^a

Causes of succession	Controlling processes	Modifying factors
Site availability	Disturbance	Size, severity, time intervals, patchiness, predisturbance history
Species availability	Dispersal	Dispersal mechanisms and landscape features
	Propagules	Land use, disturbance interval, species life history
Species performance	Resources	Soil, topography, climate, site history, microbes, litter retention
	Ecophysiology	Germination requirements, assimilation rates, growth rates, genetic differentiation
	Life history	Allocation, reproduction timing and degree
	Stress	Climate, site history, prior occupants, herbivory, natural enemies
	Interference	Competition, herbivory, allelopathy, resource availability, predators, other level interactions

^a Modified from Pickett et al. (1987).

to half of every plot with a backpack sprayer. In late October 2002, plots were rototilled to a depth of 5 cm, and plots were broadcast seeded at a rate of 34 kg/ha. The seed mixture consisted of six grasses (17 kg/ha) and five forbs (17 kg/ha), including bluebunch wheatgrass (5 kg/ha), rough fescue (5 kg/ha), prairie junegrass (Koeleria cristata Pers.) (1.75 kg/ha), Baltic rush (Juncus balticus Willd.) (1.75 kg/ha), Sandburg's bluegrass (Poa sandbergii Vasey) (1.75 kg/ha), western wheatgrass (Agropyron smithii Rydb.) (1.75 kg/ha), indian blanket flower (Gaillardia aristata Pursh.) (3.4 kg/ha), sticky geranium (Geranium viscosissimum F. & M.) (3.4 kg/ha), common yarrow (Achillea millefolium L.) (3.4 kg/ha), silky lupine (Lupinus sericeus Pursh) (3.4 kg/ha), and wild bergamot (Monarda fistulosa L.) (3.4 kg/ha). These species represented key functional groups within the habitat type. In May, June, and July 2003, watering treatments were applied so that one-third (135 mm) the average annual precipitation (400 mm) was added.

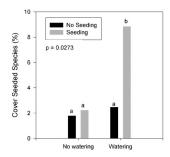
Sampling. Plots were sampled for percent bare ground and percent soil moisture in 2002 before treatments were added and again in 2003 after treatments were added. Percent bare ground was estimated in July within two randomly placed Daubenmire frames (0.10 m²) per subplot. Percent soil moisture was sampled in three random locations per whole plot from May to August within the upper 15 cm of the soil profile using time domain reflectometry (Jones et al. 2002). Cover and density of seeded species, spotted knapweed, and sulfur cinquefoil were estimated in July 2002 before treatments were added and again in July 2003 after treatments were added. Percent cover and density of plant species were estimated within two randomly placed Daubenmire frames (0.10 m²) in each subplot.

Data Analysis. ANOVA was used to determine plot to plot variation in soil moisture before treatments were added. After treatments were added, ANOVA was used to determine the response of watering on soil moisture.

ANOVA was used to determine plot to plot variation in percent bare ground before treatments were added. Analysis of covariance (ANCOVA) was used to determine the response of seeding, watering, and shallow tilling on seeded species, spotted knapweed, and sulfur cinquefoil density and cover. Pretreatment cover and density data were used as a baseline covariate. Cover and density data were square root transformed to meet assumptions of ANOVA and ANCOVA, and Fisher's LSD procedure ($\alpha = 0.05$) was used to compare means.

RESULTS AND DISCUSSION

The management of wildland systems dominated by invasive species must move toward the restoration of ecological mechanisms and processes that support the reestablishment of sustainable, invasion-resistant plant communities (Sheley and Krueger-Mangold 2003; Zavaleta et al. 2001). Augmentative restoration uses successional theory to guide the implementation of restoration strategies that use existing ecological processes that are functioning adequately by augmenting processes that are operating insufficiently. Before treatments were added, the study site had high percent bare ground (55%) because of meadow vole disturbance, low soil moisture because of the upland position (24% in May), and low cover of native species (11%). We hypothesized that site availability was adequate because of vole disturbance, but the level of soil moisture and abundance of desired species were insufficient and would require augmentation to support the establishment of a desired plant community. Our data indicated that the treatment combination of seeding and watering increased seeded species cover (P = 0.0273) from 2 to 9% and density (P < 0.0001) from 18 to 120 stems/m² (Figure 1), whereas tilling did not significantly affect seeded species cover (P = 0.9626) or density (P = 0.9236). Spotted knapweed and sulfur cinquefoil density (P = 0.0121) decreased from 50 to 20 stems/m² in response to 2,4-D.



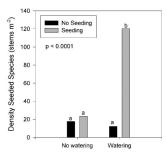


Figure 1. Percent cover and density of seeded species in response to the combination of seeding and watering treatments.

These data provided strong evidence in support of our hypotheses, indicating the importance of developing invasive plant management strategies that augment ecological mechanisms and processes when restoring desired plant communities. Further research could investigate the application of augmentative restoration to landscapes that vary spatially in factors influencing successional processes. For example, within one landscape, vole disturbances could be abundant in some areas and devoid in others (Rebollo et al. 2003), whereas soil moisture could be adequate in one area and insufficient in another (Berlow et al. 2003). Similarly, desired species abundance could be adequate for natural colonization in particular patches and devoid in others (Whisenant 1999). Augmentative restoration may provide a framework for guiding the development of treatment combinations that vary in response to the ecological variation in the landscape. This approach may preserve existing heterogeneity and diversity, which may improve the establishment and maintenance of functionally diverse, weed-resistant plant communities (Huston 1994).

Augmentative restoration may provide managers with a framework that enables them to identify variation in successional processes and to make strategic, site-specific decisions. Wildland managers often adapt farming practices uniformly across the landscape in an attempt to establish native species. Although using farming practices may be successful for establishing many nonnative species, it is becoming increasingly clear that native species require techniques based on an understanding of the ecological mechanisms and processes directing their success (Sheley and Krueger-Mangold 2003; Whisenant 1999). Our data provided initial evidence that augmentative restoration may improve our ability to establish native species on invasive plant-dominated wildlands because it addresses the ecological causes of plant succession.

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